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Leioproctus zephyr Prendergast (Hymenoptera, Colletidae, *Leioproctus*), an oligoletic new bee species with a distinctive clypeus

Kit S. Prendergast[1]

1 *School of Molecular and Life Sciences, Curtin University, Kent Street, Bentley, Perth Western Australia, 6102, Australia*

Corresponding author: Kit S. Prendergast (kit.prendergast21@gmail.com)

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Abstract
A new species *Leioproctus zephyr* (Hymenoptera: Colletidae) is described from both sexes. *Leioproctus zephyr* **sp. nov.** is remarkable in featuring a large longitudinal ridge on the clypeus. This diagnostic morphological feature present in both sexes, along with various other distinctive characters including the male genitalia, female hind-tibial spur, and glossa morphology, clearly distinguish this species from all other *Leioproctus*. Along with these unique traits, *L. zephyr* cannot be classified into any of the existing subgenera of *Leioproctus*, sharing some, but not all, of the characters of the subgenera *Ceratocolletes*, *Charicolletes*, *Protomorpha* and *Odontocolletes*. DNA barcoding with the CO1 gene confirmed the sexes belonged to the same species and it did not match any previously barcoded species. This species is restricted to native vegetation remnants in the southwest Western Australian biodiversity hotspot, and is highly specialised, foraging only on a few species in the genus *Jacksonia* (Fabaceae). The unusual clypeus may be an adaptation for foraging on the keeled papilionaceous flowers. The limited number of sites this species has been collected from and its oligolectic diet suggest *L. zephyr* should be considered to be a species of conservation concern. Further taxonomic research is required to determine the phylogenetic position of this unusual *Leioproctus*.

Keywords
Australia, biodiversity hotspot, colletid, DNA barcoding, new species, specialist

Introduction

The genus *Leioproctus* Smith 1853 (Colletidae Lepeletier 1841), as currently described, is a highly diverse, speciose taxon (Almeida and Daforth 2009; Engel and Gonzalez 2022). In Australia, it is distributed throughout most of the continent, and the most recent guide to native bees of Australia divides this genus into 24 subgenera, with 193 named species (Houston, 2018), yet with hundreds awaiting description (Houston, personal comm.). New species are continually being described (e.g., Batley and Popic 2013; Leijs et al. 2018).

The systematics of *Leioproctus* requires clarification (Packer 2006; Almeida et al. 2019). A phylogeny combining morphological and molecular data of currently recognised subgenera is yet forthcoming. Even *Leioproctus* s. str. appears to be paraphyletic based on molecular phylogenies (Almeida and Danforth 2009; Almeida et al. 2019). In the magnum opus on the classification of native bees, Michener (2007) drew attention to how the sub-genera of Australian *Leioproctus* can be ill-defined, with partial intergradation among some taxa, as evident in the last revision of seven subgenera of *Leioproctus* (Maynard, 2013), A comprehensive and more thorough understanding of the Australian subgenera is hampered by the sheer diversity of many unusual species that are undescribed, and even of those that are described, many are described from only one sex. It is clear that an updated classification for the Australian Neopasiphaeinae is needed (Almeida et al. 2019; Engel and Gonzalez 2022). A new species, with a distinctive clypeus, that does not fit neatly into an existing subgenus is described, including its CO1 barcode, and data on its restrictive foraging and distribution range. This description will contribute to documenting and describing the diversity of Australian Neopasiphaeinae.

Materials and methods

Specimens involved in the description were collected by the author with an entomological sweep-net (bag mesh size 0.9 × 0.3mm, Australian Entomological Supplies Pty Ltd) during surveys to sample native bee assemblages in residential gardens and bushland remnants within the urbanised region of the southwest Western Australian biodiversity hotspot (Prendergast et al. 2022; Suppl. material 1). The unusual appearance of this species and an inability to key the species out to subgeneric or species level from published keys led the author to contact Dr Terry Houston of the WA Museum to inquire whether he had seen this species before. This species was confirmed to be undescribed, lodged in the WA Museum and catalogued as *Leioproctus* (*Protomorpha*?) F188/M173. Further consultation with Dr Glynn Maynard who undertook the most recent revision of Australian *Leioproctus* (in part, Maynard 2013) confirmed that these specimens did not match described species.

Standard melittological terminology is used to describe the morphology (Michener, 2007). The following standard acronyms are used (following Michener (2007), Houston (1990) and Leijs et al. (2018)): **HL** head length; **HW** head width; **AOD** antennocular distance; **IAD** interantennal distance; **OOD** ocellocular distance; **OAD** ocelloantennal distance; metasomal sterna and terga are denoted **S**[segment number] and **T**[segment number], and flagellomeres are denoted **F**.

Following Packer (2006), the relative diameter and spacing for punctures (sculpture) are denoted by d and i, respectively. Other types of surface sculpturing follow Houston (Houston, 1975), as used in (Leijs et al. 2018). Measurements of key morphological features and relative head measurements were made on five specimens of each sex and averaged, and given in millimetres (Suppl. material 2). Specimens were observed with a Leica M205 C stereomicroscope, and measurements were made on high-resolution images taken with the same stereomicroscope and using the Leica auto-montage image stacking software. Images of key features were taken using a Nikon camera with Passport and Helicon image stacking software.

A sample (hind femur) of the female and male type and allotype were submitted to BOLD (Barcode of Life Database) for DNA barcoding using the cytochrome c oxidase subunit 1 (CO1) gene. The DNA barcode sequence, and other specimen information associated, can be accessed in BOLD via: as part of the Australasian and Pacific bee fauna Project (MSAPB): http://www.boldsystems.org/index.php/MAS_Management_DataConsole?codes=MSAPB.

The sequences were obtained from Canadian Centre for DNA Barcoding (CCDB) at the University of Guelph, Guelph, Ontario, Canada. Standard DNA sequencing protocols were carried out by CCDB (available online at: http://www.ccdb.ca/resources.php), using the PCR primers LepF1/LepR1. The barcoded vouchers are housed at the Museum of Western Australia. BOLD delineates molecular operational taxonomic units (MOTUs), which typically are in close concordance with species delineations based on traditional methods (Schmidt et al. 2015). The barcode index number (BIN) (Ratnasingham and Hebert 2013) is automatically assigned to a MOTU, which is incorporated into BOLD.

To ascertain the position of this species in relation to other *Leioproctus* and infer its placement within one of the described subgenera, a Taxon ID tree was created in BOLD using all specimens in the AUSBS project. The Taxon ID tree procedure uses varied distance metrics to generate a neighbour-joining (NJ) tree based on nucleotide similarity in the barcoded COI gene. Sequence alignment is automatically handled, with the Kimura 2 Parameter as the default distance model.

Taxonomy

Family Colletidae Lepeletier, 1841
Subfamily Neopasiphaeinae

Genus *Leioproctus* Smith, 1853

Type species. *Leioproctus imitatus* Smith, 1853.

Leioproctus zephyr sp. nov. can be assigned to the genus *Leioproctus* based on the following diagnostic features: facial fovea broad, moderately impressed; mandibles with only one subapical tooth, with the rutellum the largest and longest; labrum more than three times as wide as it is long; stigma well-developed, tapering apically to marginal

vein, well within the marginal cell; propodeum with sloping, subhorizontal basal zone; inner hind tibial spur of the female pectinate, not crowded; basitibial plate of the female well-defined.

This species cannot be clearly assigned to the currently recognised subgenera of *Leioproctus*. Although this species shares various features of the two species currently assigned to the subgenus *Ceratocolletes* Michener, 1965, *L. zephyr* diverges in details of the hind-tibial spurs, propodeum, and male genitalia, and whilst it shares similarity in the clypeus morphology of *L.* (*Ceratocolletes*) *antennatus* Smith, 1879, it lacks the modified antennae of the male. The species also shares some diagnostic characters of *Protomorpha* Rayment, 1959, *Charicolletes* Maynard, 2013, and *Odontocolletes* Maynard, 1997, such as the malar space absent; strong punctures on the dorsal surface of the mesosoma with smooth interspaces; terga with pale apical hair bands; flagellum short, middle segments mostly broader than long or scarcely longer than broad; clypeus and supraclypeal area not flat, usually punctate, suture separating the m distinct; S7 of the male has two apical lobes. However, it lacks other diagnostic features, and has features unique to it and absent in these subgenera. On this basis, *L. zephyr* cannot be confidently assigned to any of the current subgenera of *Leioproctus.* This species may represent a new subgenus of *Leioproctus*, however but a revision of these subgenera and species currently assigned to them is required.

***Leioproctus zephyr* Prendergast, sp. nov.**
https://zoobank.org/7C496A48-0D63-43AF-802A-9B8C5B144BF8
Figs 1–7 (female), 8–15 (male)

Material examined. ***Holotype*** female, allotype male, 60 additional male ***paratypes*** and 52 female paratypes : Australia, Western Australia.

Type-locality. Australia, Western Australia: Western Australia, Star Swamp; 31.8575°S, 115.7602°E; alt. *ca.* 11 m, Banksia woodland, collected with an entomological sweepnet, foraging on *Jacksonia sericea*, 16 Dec 2017, K. Prendergast.

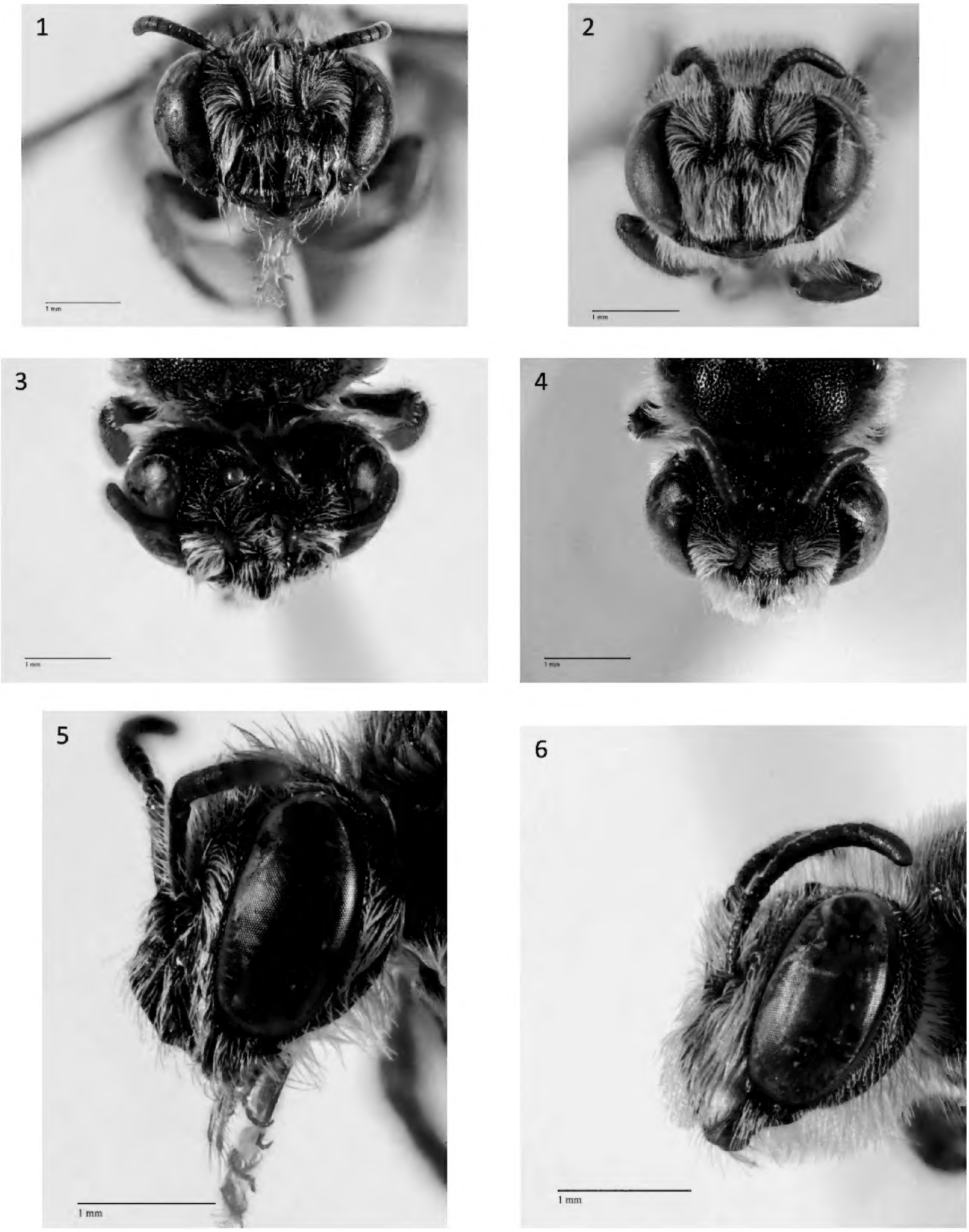
Type-specimen. Holotype female, pinned, with the printed label: "WA: Western Australia, Star Swamp 31.8575°S, 115.7602°E 16/12/2017 Sweepnet AM 0003436 K. S. Prendergast" (WAM).

Type material. ***Holotype*** Australia • 1 ♀, holotype; Western Australia, Western Australia, Star Swamp; 31.8575°S, 115.7602°E; alt. *ca.* 11 m; 16 Dec. 2017; K. S. Prendergast leg.; sweepnet; KSP code 003436. BOLD DNA barcode: BOLD:AEC1713 (WAM).

Other material. ***Allotype*** Australia • 1 ♂; Western Australia, Star Swamp; 31.8575°S, 115.7602°E; alt. ca. 11 m; 3 Dec. 2016; K. S. Prendergast leg.; sweepnet; KSP code 000261. BOLD DNA barcode: BOLD:AEC1713 (WAM).

Paratypes. Paratypes listed in Suppl. material 1. Paratype used in description of male S7, S8 and genital capsule: • 1 ♂ same data as for allotype.

All specimens were collected with an entomological sweep-net by K. Prendergast (Suppl. material 1).



Figures 1–6. *Leioproctus zephyr* sp. nov., emphasising the protruberant clypeus. Frontal view **1** female **2** male; dorsal view **3** female **4** male; lateral view **5** female **6** male. Photographs by N. Tatarnic.

The holotype, allotype and paratype specimens are bequeathed to the Western Australian Museum.

Diagnosis. *Leioproctus zephyr* is distinguished from all other species of the genus in that both sexes are easily distinguished by the presence of a large medial ridge extend-

ing the length of the clypeus with a large, prominent protuberance on the upper half (Figs 1–6). Females are unique in having a pectinate inner hind tibial spur featuring a blunt apex (Fig. 14). Male genitalia are also unique in S7 with two broad, flat apical lobes orientated laterally, fringed with hair, with particularly long hairs on the apical edge; posterior lobes of S7 extended laterally with broad, flat flanges (Fig. 22); S8 with large lateral lobes extending beyond the breadth of the apical process; apical process broad, somewhat narrowed towards base, and hirsute, with apex expanded, rounded and membranous (Fig. 28). The glossa of both sexes are also distinctive, being more bifurcated than is typical for most Australian *Leioproctus*. Additionally, in *L. zephyr*, labial and maxillary palps are comparatively short, as they do not reach the base of the prementum or apex of paraglossa, respectively; this contrasts with most *Leioproctus* where the labial and maxillary palps extend just beyond apex of the glossa..

Description. Female (Figs 7–14):

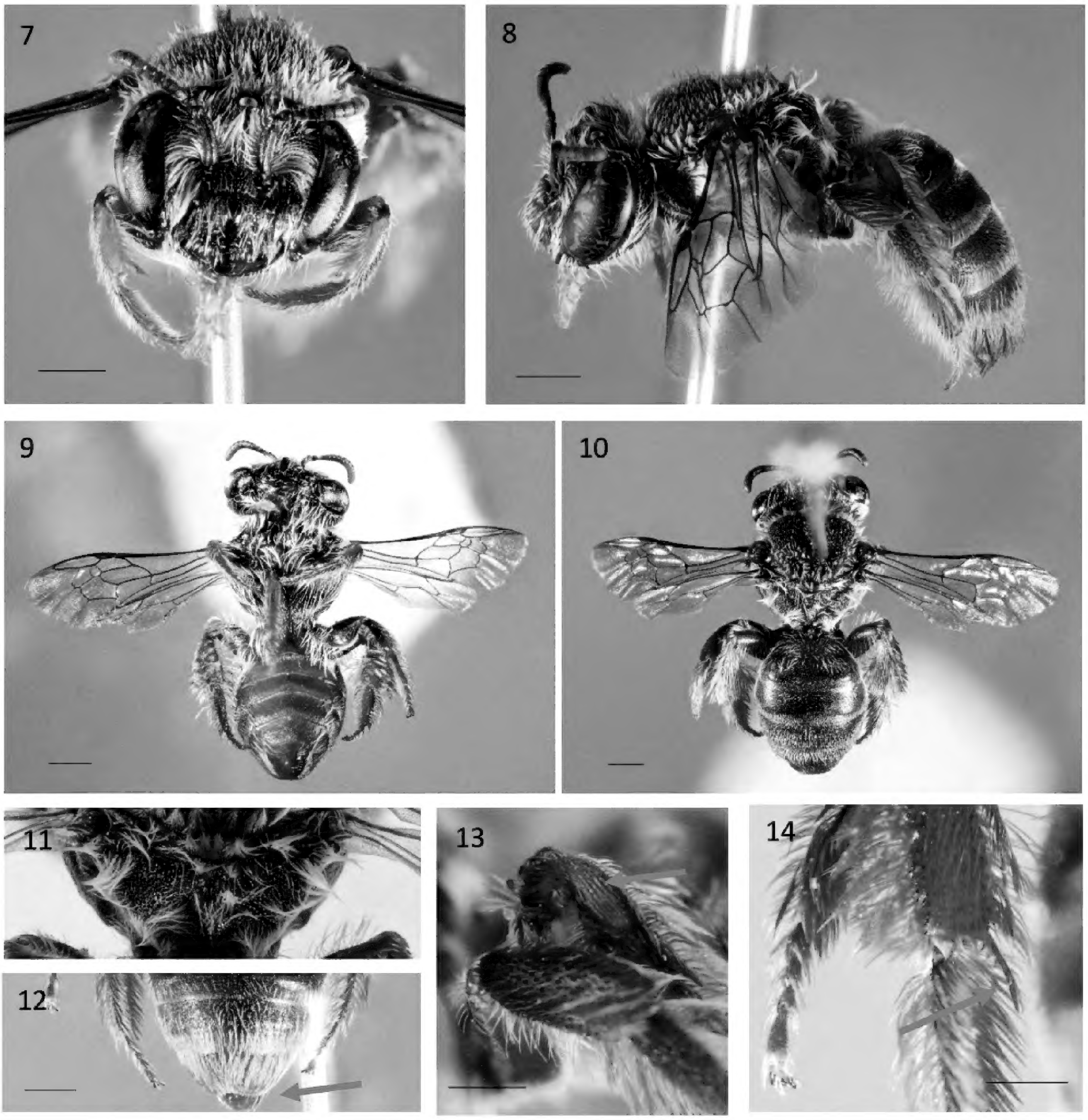
***Dimensions*:** Total body length 6.2 mm, HW 2.2 mm, ITD 1.6 mm (variation: total body length 6.0–6.9 mm, HW 2.1–2.2 mm, ITD 1.5–1.6 mm (n = 5)).

***Colouration*:** Non-metallic black; integument of head black; facial protuberance black, but sometimes with reddish tinge tip of protuberance; mesosoma black; terga and sternum black apically through to brown on posterior margin; apical impressed area of T1 brown; T6 and pygidial plate brown; legs and tarsi brown; wings dusky, semi-opaque very dark brown with wing veins very dark brown; scape and flagellum black except for F10, and part of F9, mandibles black basally, rest mostly testaceous, except apex black.

***Pubescence*:** White pubescence on face around antennal sockets covering paraocular area and gena, sides of thorax; sparser setae on supraclypeal area, and each side medial carina along the transverse portion of the epistomal suture. Short, fine sparse pale orange hairs on vertex, mesosomal dorsum (mesoscutum, scutellum, and propodeum), thicker, longer on metanotum; thick dense cream hairs on pronotal lobe; sparse long pale brown hairs on T3 and T4 on lower half, incomplete medially; on T5 gold-brown hairs very dense; prepygidial fimbria thick, dense pale brown hairs either side of pygidial plate. Apical fringe of long gold-brown hairs towards sides of S1-S6. Shorter orange hairs on legs, longer white hairs on posterior margin of forefemur. Hairs on forelegs long and dense, especially on basitarsus; midtarsal hairs branching in a V-pattern. Pubescence never obscuring integument below.

***Sculpture*:** Head, mesoscutum, and scutellum with large, deep, close punctures i=1d; punctures open, sparse on clypeus i=5d, except impunctate on median carina; antennal scape fine, close punctures i=1d; metanotum and propodeum with small, close punctures; propodeal triangle with deep, sparse punctures apically i=3d, lower propodeal triangle imbricated (Fig. 11); terga with shallow, minute, close punctures i=1d; fore-, mid- and hind- femur, tarsus and basitarsus with longitudinal, large, irregular striae i=1d.

***Structure*: *head*:** face wider than long (1.6×); ocelloccipital area weakly concave; mouthparts distinctive: galea large and strongly bifurcate, each fork reaching just above the base of the mentum and with long, golden hairs; mentum and prementum



Figures 7–14. *Leioproctus zephyr* sp. nov., female. **7** Head, frontal view **8** Lateral habitus **9** ventral view **10** dorsal view **11** propodeal triangle **12** pygidial plate **13** basitarsal plate **14** inner hindtibial spur. Scale bars: 1 mm (**1–5**); 0.5 mm (**6–7**). Photographs by K.S. Prendergast.

approximately equal in length; maxillary palpus extremely short, not reaching base of prementum and labial palps short, not reaching apex of paraglossa; paraglossa large, triangular; glossa strongly bifurcate, more so than in most Australian *Leioproctus*, with a long, dense apical fringe; clypeus convex, broader than long, with a medial longitudinal ridge and distinct protuberance in middle of upper half, protuberance triangular in profile, apex above clypeal midlength and almost one quarter length of head, with smaller protuberance at base of median ridge; clypeus lateral to this medial ridge and below epistomal suture convex; supraclypeal area elevated, surface concave, somewhat triangular; frontal line continuous with median ridge strongest at level of antennal sockets, extending to the medial ocellus; compound eyes slightly more convergent

below; malar space absent; mandibles bidentate, with the preapical tooth being approximately half length of rutellum; mandibles with acetabular and condylar grooves, outer and condylar ridge absent; facial fovea impressed, smooth, from lower tangent of lateral ocelli extending to level with lower tangent of antennal sockets, forming a triangular shape, broadest at level just below median ocellus, impression deepest adjacent to eye; gena ca. 0.4× as wide as compound eye viewed laterally; scape not attaining median ocellus; F1 length>width, F2-F10 length<width, tip of antennae slightly pointed.

Head measurements: HW 2.14 mm; eye width in profile 0.61 mm; gena width 0.22 mm; eye length 1.25 mm; HL 1.38 mm; clypeus length 0.63 mm; LOD 1.11 mm; UOD 1.20 mm; clypeoantennal distance 0.07 mm; IAD 0.38 mm; IOD 0.38 mm; OOD 0.29 mm; AOD 0.47 mm; OAD distance 0.33 mm (variation: HW 2.08 – 2.15 mm; eye width in profile 0.52–0.62 mm; gena width 0.18–0.26 mm; eye length 1.18–1.26 mm; HL 1.37–1.55 mm; clypeus length 0.46–0.63 mm; LOD 0.45–1.11 mm; UOD 1.14–1.22 mm; clypeoantennal distance 0.15–0.18 mm; IAD 0.36–0.39 mm; IOD 0.31–0.38 mm; OOD 0.30–0.38 mm; AOD 0.47–0.66 mm; OAD distance 0.32–0.40 mm, n = 5).

Relative head measurements: UOD:LOD 1.23; OOD:IOD 0.93; clypeus:HL 0.35.

***Mesosoma*:** overall mesosoma length 2.12 mm; pronotal collar absent; ITD 1.60 mm; mesoscutum length 1.60 mm; mesoscutum width 1.52 mm; metanotum length 0.18 mm; propodeum length 0.41 mm (variation: overall mesosoma length 1.89–2.12 ± 0.03 mm; pronotal collar absent; ITD 1.54–1.61 mm; mesoscutum length 1.00–1.57 mm; mesoscutum width 1.46–1.60 mm; metanotum length 0.14–0.20 mm; propodeum length 0.31–0.50 mm, n = 5).

Forewing with three submarginal cells, with second sub-marginal cell much shorter than the first and third. Propodeal triangle with strong carina, almost vertical.

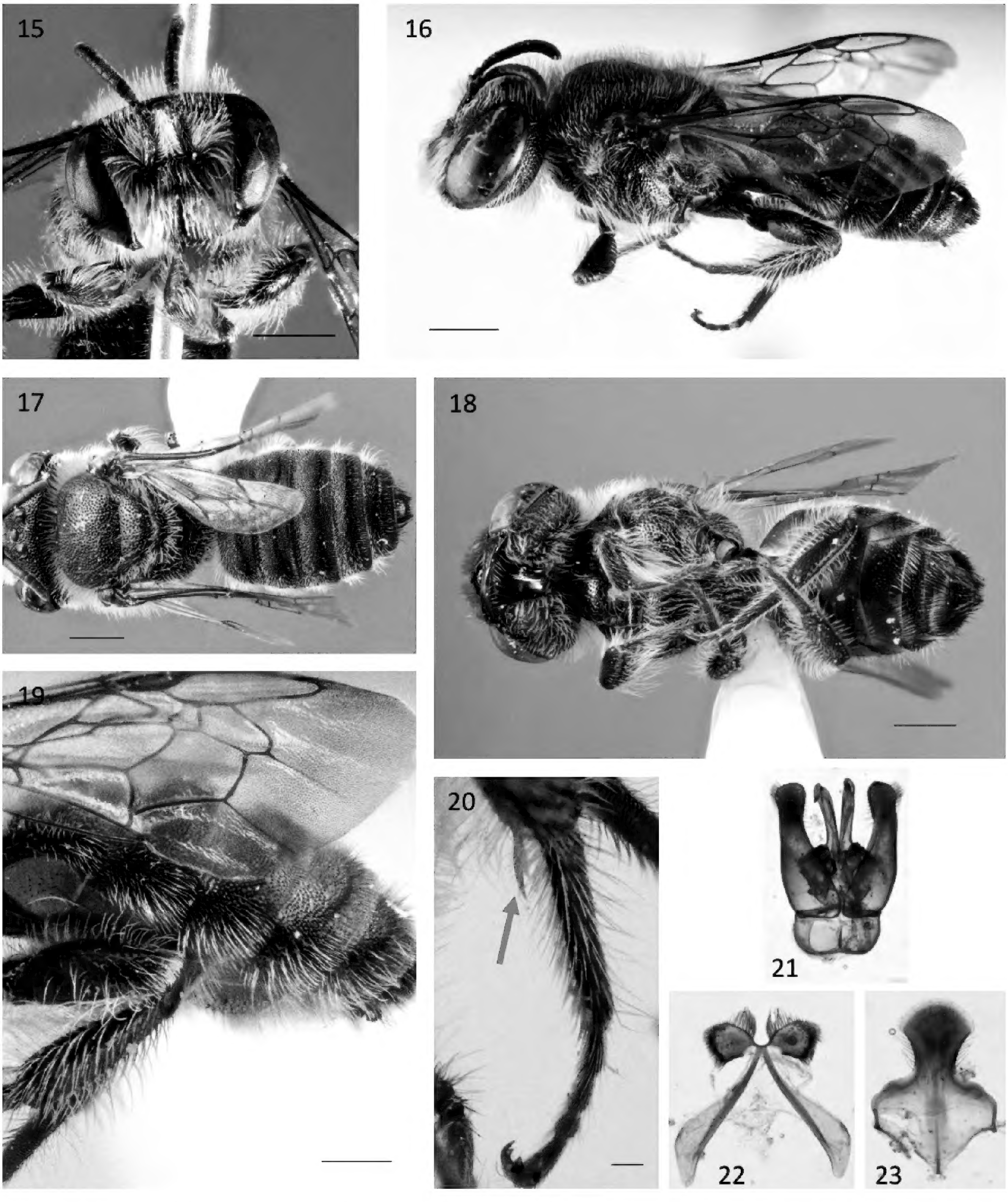
Relative mesosomal structure measurements: mesoscutum length:breadth 0.84; scutellum:mesoscutum 0.28; metanotum:scutellum 0.53.

***Legs*:** tarsal claws on all legs simple; basitibial plate approximately one-quarter as long as basitarsus, oval, concave, covered with dense short orange hairs (Fig. 13); metatibial spur long, almost straight, outer spur with small, dense serrations, inner spur pectinate with four teeth on basal half of the spur, decreasing in length from base to apex, the second tooth from the base thickest, apex of spur rounded (Fig. 14).

***Wings*:** stigma approximately half the length of the marginal cell; marginal cell with apex rounded, curved away from costal wing margin by approximately two vein widths; basal vein slightly curved and at approximately 45° to costal wing margin; three submarginal cells, first longest, and second shortest; first recurrent vein slightly basal to first submarginal cross-vein; jugal lobe of hind wing approximately one-quarter as long as vannal lobe, reaches cu-a vein.

***Metasoma*:** overall metasoma length 3.1 mm (variation: 3.15 ± 0.116 mm); metasoma longer than mesosoma (metasoma:mesosoma 1.55); T1 declivous surface concave with longitudinal medial groove just below point of concavity; anterior declivous surface longer than dorsal horizontal portion; metasoma broadest at second segment, width 1.98mm (variation 1.97 ± 0.014 mm); pygidial plate well-developed, smooth.

Male (Figs 17–23):



Figures 15–23. *Leioproctus zephyr* sp. nov, male **15** head, frontal view **16** lateral habitus **17** dorsal view **18** ventral view **19** forewing vein structure **20** hindleg showing hindtibial spurs **21** male genital capsule (dorsal view) **22** S7 (ventral view) **23** S8 (ventral view). Scale bars: 1 mm. Photographs by K. S. Prendergast, diagrams by K. S. Prendergast.

***Dimensions*:** Total body length 5.01–5.71 mm, HW 1.07–1.97 mm, ITD 1.30–1.41 mm (n = 5).

***Colouration*:** integument black except for foreleg basitarsus which is orange-brown; antennal scape black, flagellomeres 1 and 2 black, flagellomere 3 partly black and partly brown, and flagellomeres 4–11 brown; mandibles black with orange-brown tips; tergites black with posterior margin brown.

***Pubescence*:** Pubescence on face much thicker than female, hairs cover entire head except for carina and protuberance on clypeus; very short, sparse hairs on basal margin of clypeus; pubescence on pronotal lobes not as thick as female; long white hairs on tarsi of fore and mid legs. Orange-brown short hairs on vertex and dorsal region of mesosoma, as in female, but much shorter and sparser, whereas white hairs on metanotum, propodeum, and metepisternum are longer, and feathery; very short brown hairs emerging along posterior region of each tergite, and longer white hairs from the anterior and laterally on each tergite; fringe of white hairs from sternites 1–5, very thick and black-tipped on T6; wings same as female.

***Sculpture*:** similar to female, except legs only have sparse, small punctures.

***Structure – head*:** prominent medial carina on the clypeus with a prominent protuberance on upper half of clypeus, extent of protuberance from face relatively more pronounced than in the female with length of protuberance:length of head 0.29; gena ca. 0.49× as wide as compound eye viewed laterally; eyes converging somewhat below; UOD:LOD 1.21; mandibles similar to female; facial fovea most depressed near eye, narrower than in female oblong in shape.

***Head measurements*:** HW 1.07–1.97 mm; eye width in profile 0.52–0.59 mm; gena width 0.26–0.33 mm; eye length 1.07–1.17 mm; HL 1.14–1.44 mm; clypeus length 0.49–0.57 mm; LOD 0.88–0.96 mm; UOD 1.07–1.15 mm; clypeoantennal distance 0.10–0.17 mm; IAD 0.30–0.33 mm; IOD 0.39–0.34 mm; OOD 0.24–0.30 mm; OAD 0.36–0.51 mm; AOD 0.27–0.29 mm (n = 5).

***Relative head measurements*:** UOD:LOD 1.21; OOD:IOD 0.82; clypeus:HL 0.41.

***Mesosoma*:** overall mesosoma length 1.71–1.92 mm; pronotal collar absent; ITD 1.30–1.41 mm; mesoscutum length 0.82–1.80 mm; mesoscutum width 1.24–1.41 mm; metanotum length 0.12–0.19 mm; propodeum length 0.27–0.46 mm (n = 5).

***Relative mesasomal structure measurements*:** mesoscutum length:breadth 1.02; scutellum:mesoscutum 0.28; metanotum:scutellum 0.43.

***Structure – legs*:** tarsal claws simple. Pair of almost straight hind tibial spurs. Inner-spur slightly longer, thicker than outer-spur.

***Structure*: *metasoma*:** metasoma longer than mesosoma, less so than female (metasoma:mesosoma 1.24); broadest at second segment, S7 two broad, flat apical lobes orientated laterally, fringed with hair, with particularly long hairs on the apical edge; posterior lobes of S7 extended laterally with broad, flat flanges, >3× length of apical lobes (Fig. 22); S8 with large lateral lobes extending beyond the breadth of the apical process; apical process broad, somewhat narrowed towards base, and hirsute, with apex expanded, rounded and membranous (Fig. 23); penis valves slightly longer than gonostylus and about half the width of the gonostylus; apex of gonostylus hirsute and rounded; gonobase about half as long as wide, with each half curved to look like a bum (Fig. 21).

Etymology. The species is named after the author's beloved Maremma dog, Zephyr. The name "zephyr" is proposed as a noun in apposition.

Distribution. Southwest Western Australia (Fig. 24).

Figure 24. Map of Australia showing sites where specimens of *Leioproctus zephyr* sp. nov. has been collected, with close-up of locations. Green locations: collection localities by the author in 2016–18; red localities: collection locations by T. F. Houston 1979, 1992, 1996, 1997. Refer to Table 1 for further information. Map produced via the online program MapCustomizer: https://www.mapcustomizer.com/.

Ecology. Months collected: Dec – Jan. Earliest collection date by the author 3-Dec 2016, latest collection date 8-Jan 2017. The latest date collected was 29-Jan 1979. **Floral visitation:** Most visitation records have been from *Jacksonia sericea* Bentham (Fabaceae) (Suppl. material 1). The species has previously been collected mainly from *J. sericea*, with three records of bees visiting *J. eremodendron* E. Pritz, and one record of a bee visiting *J. horrida* (de Candolle) (however, based on how the distribution of *J. horrida* does not extend north to where the bee was collected, this is likely a misattribution and this collection record was also from *J. sericea* (Western Australian Herbarium 2022) (Suppl. material 1).

Conservation status. The species has only been collected at six sites, all of which are in parks or reserves (Fig. 24, Suppl. material 1). Recent systematic surveys across twenty-one sites over an area of ca. 300 km^2 revealed the species to only occupy four of these. On the basis of all known records to date, the total area of occupancy is ca. 40 km^2, and this habitat is fragmented by urban development. The species has also been collected at one other site within this region, as well as another site widely separated from the others some 200 km north. The species is presumably oligolectic on a small number of *Jacksonia* species, with the two main confirmed hosts also having a narrow distribution restricted to the Swan Coastal Plain (Western Australian Herbarium 2022) As no nests have been recorded, its nesting requirements are unknown, other than that it would be a ground-nesting species (Almeida, 2008). All populations however were recorded on the well-drained and weathered sandy soils of the Swan Coastal Plain (MacArthur, 2004), and thus it may be a psammophile. As a ground-nesting bee, it is sensitive to destruction of nesting habitat due to road-building and development that leads to impervious surfaces.

Under the IUCN Red List criteria, criteria A, C and E cannot be assessed as there is no ongoing monitoring; however, based on criteria B: Geographic range in the form of either B1 (extent of occurrence) OR B2 (area of occupancy) OR both, it may be considered to be vulnerable to extinction in that: Extent of occurrence is estimated to be less than 20,000 km^2, and estimates indicate habitat in which it has been recorded is severely fragmented or known to exist at no more than 10 locations (IUCN, 2012).

DNA barcoding. DNA barcoding confirmed that that male and female specimens collected were the same species, with both the male and three specimens which were successfully sequenced receiving the BOLD BIN number BOLD:AEC1713 (http://www.boldsystems.org/index.php/Public_BarcodeCluster?clusteruri=BOLD:AEC1713). A tree of sequences generated from the MSAPB sequences (involving a total of 4136 specimens of 169 Australian bee species) places this species in an undefined group with four other *Leioproctus* species, all of which include species that do not appear to have been scientifically described.

Discussion

This new *Leioproctus* species is highly distinctive in its morphology. It does not conform to any of the subgenera in the latest revision (Maynard, 2014). This morphological distinctiveness of this species was supported from DNA barcoding studies. This species was in a cluster with four other species (none of which appear to have been formally described), with an average distance of about 15%. The closest species from an NJ tree based on sequenced species is an undescribed *Leioproctus* (*Leioproctus sp.* "CH13"). It appears that the ridge is an autapomorphy, as none of the species in this clade have a ridge on the clypeus or a blunt thick apex of the hind tibial spur. Dissections of genitalia of the males revealed the S7 is comparatively simple for *L. zephyr*, being more complex in these other species. The only distinctive trait of *L. zephyr* shared with these other species is the short, robust S8 (R. Leijs, personal communication, 2020). Although sequencing with a single gene is insufficient to accurately represent evolutionary relationships, on the basis of these results it appears that clypeal protuberances can be homoplastic and represent convergent evolution in *L. zephyr* and *Leioproctus* (*Ceratocolletes*).

In the WA Museum collection database, Houston tentatively placed this undescribed species in the subgenus *L.* (*Protomorpha*), however although this species exhibits some features characteristic of this subgenus (namely terga with pale apical hair bands; flagellum short, middle segments mostly broader than long or scarcely longer than broad; clypeus and supraclypeal area not flat, usually punctate, suture separating them distinct), other key features of *Protomorpha*, are lacking, including: females with striate pygidial plate (pygidial plate lacks any ornamentation or sculpturing); males with hind tibia and basitarsus elaborately expanded (no elaborations on these leg segments, tibia only slightly broader than is typical for male *Leioproctus*, no expansion of the basitarsus); males with robust body like that of females (although robust compared with some *Leioproctus* subgenera, female is distinctly more robust than the male); S7 of male with

two large apical lobes (lobes, although present, are greatly reduced); mandibles simple, sharply pointed, without preapical tooth (mandibles broad, blunt, with preapical tooth); propodeum shorter than metanotum (propodeum is longer than metanotum). Similarly, this species exhibits features of *Odontocolletes* (which has features that are consistent with most of the major external features of *Protomorpha*), including the malar space absent, strong punctures on the dorsal surface of the mesosoma with smooth interspaces; it is also from the same geographic region as the majority of *L.* (*Odontocolletes*) species (Michener 2007; Maynard 2013). However, it lacks other key diagnostic traits, including red terga lacking apical hair bands and the diagnostic feature of *Odontocolletes* of a large, blunt, median tubercle on the metanotum (Michener 2007; Maynard 2014). And whilst like these subgenera, S7 of the male has two apical lobes, these wouldn't be considered "large", as is the case for *Protomorpha* and *Odontocolletes.* It also features some similarities with *Charicolletes* as described by Maynard (2013), including impressed facial fovea, strong punctures, and short antennal scapes. However, it is not metallic like *Charicolletes*, nor does it have a median metanotum tubercle. The morphologies of S7 and S8 of *L. zephyr* do not match those of the taxa illustrated in Maynard (2013). Whilst a number of taxa have two broad, flat apical lobes oriented laterally, few are as short in relation to the ventral processes, nor are they the same shape, as that of *L. zephyr*. Interestingly, S7 of *L. zephyr* is most similar to that of *Goniocolletes parvus* Maynard, 2013, however S8 and the genital capsule are morphologically dissimilar (compare with fig. 217–219 in Maynard (2013)). The genital morphology also bears some similarity to *L.* (*Exleycolletes*) *argentifrons* Smith, 1979 and *L.* (*Leioproctus*) *macmillani* Houston, 1991, but the ventral lobes are not as long in relation to the apical lobes, and distribution of hairs on the apical lobes are dissimilar, and the apical portion of S8 is narrower (see Maynard 2013, figs 48–49, 121–122). This species shares features with the subgenus *Ceratocolletes*, and appears to be most closely related to this genus, in being a stout-bodied, strongly punctate colletid; surface sculpture, on the metasoma in particular, having small, strong punctures with clearly defined, polished interspaces; the second to fourth metasomal terga in females and second to fifth metasomal terga in males with white, apical bands; malar space absent, and, notably, the clypeus with narrow, longitudinal, median, glabrous area (obscured by hair in males) (Maynard, 1993). However, unlike *Ceratocolletes* there is no distinct horizontal basal area on the propodeum and the basal area is not rounded onto the vertical area, and the propodeum in punctured, rather than smooth; in addition the scape does not attain the level of the median ocellus (Maynard 1993; Michener 2007). In the key to subgenera of *Leioproctus* with three submarginal cells by Maynard (2014), *Ceratocolletes* is separated along with *Lamprocolletes* and *L. opaculus* Cockerell 1929 from all other subgenera in having the jugal lobe of the hindwing not reaching cu-a. In *L. zephyr*, the tip of the jugal lobe extends just past the cu-a vein. The inner hind tibial spur of the female is also distinctly blunt and, unlike *Ceratocolletes*, does not have 11 long, fine teeth (Maynard 1993), instead having three blunt prongs only on the proximal section of the spur (see Fig. 7). The female's pygidial plate is also not narrow and convex (Maynard 2014). The current species lacks the diagnostic paired lateral lobes on the male seventh sternum, and instead has only a single lateral lobe, and

other features of the genitalia exhibit degrees of difference from *Ceratocolletes*. Only two species are currently recognised as belonging to *Ceratocolletes*. *L.* (*Ceratocolletes*) *xanthosus* Maynard 1993 has been collected from two areas in eastern Australia, and differs from the current species in the above differences related to the subgenus, as well as yellow colouration, golden hair in the males, and although the clypeus of the female is convex with a median ridge, it is not strongly protuberant (Maynard, 1993). The other species, *Leioproctus* (*Ceratocolletes*) *antennatus* also occurs only in southwest WA like *L. zephyr* and the apical hair bands on the terga in the female are incomplete medially (although these are also incomplete in the male of *L. zephyr*). However, in addition to the above differences at the subgeneric level, and like *L.* (*Ceratocolletes*) *xanthosus*, the antennae have yellow colouration, and males of *L.* (*Ceratocolletes*) *antennatus* have antennae with the apical segment expanded and flattened, in contrast to the unmodified antennae of *L. zephyr*. This unusual modification of the male's antennae however is an autapomorphy and is absent in *L.* (*Ceratocolletes*) *xanthosus.* In Michener (2007)'s description of this subgenus, he notes that hind legs of the male are incrassate, trochanters toothed, tibiae bent, and tibial spurs reduced in size-features absent in *L. zephyr*, however it is noted that these features of the male's hindlegs are only in one of the species, but which of the two species is not mentioned, and the description of *Ceratocolletes* by Maynard (1993) does not include these features. Although the first description of *Ceratocolletes* included a medially protuberant clypeus as a diagnostic feature of this subgenus (Michener, 1965), Maynard (1993), in placing *L. xanthosus* into *Ceratocolletes*, suggested that this feature was no longer subgenerically significant.

Like *L. zephyr*, both *Ceratocolletes* have only been collected on Fabaceae: *Pultanaea* spp. for *L.* (*Ceratocolletes*) *xanthosus*, and as with *L. zephyr*, *L.* (*Ceratocolletes*) *antennatus* have been recorded exclusively foraging on *Jacksonia* (Houston, 2000).

Looking at its phylogenetic relationships and cladistics groupings based on the Taxon ID Tree functionality in BOLD, the dendrogram generated from sequencing using the neighbour joining algorithm was not able to resolve its subgeneric grouping. Rather, it suggests that *L. zephyr* belongs to a distinct clade with a number of other undescribed *Leioproctus* (Mark Stevens, Remko Leijs, pers. comm. March 2022). The closest scientifically-described species were *Leioproctus conospermi* Houston 1989 (Supporting Information3), – an oligolectic species that features highly modified features as adaptations for foraging on the host, *Conospermum* (Houston, 1989), and *Leioproctus excubitor* Houston 1991, which has highly modified antennae in the male (Houston, 2018). Both of these species are currently placed in the subgenus *Leioproctus.* As such, the various features outlined above that *L. zerphyr* shares with various other subgenera (*Protomorpha* and *Cladocerapis*) are not taxonomically informative. It should be noted that phylogenetic analyses involving more than just the CO1 gene are required to further elucidate the taxonomic placement of *L. zephyr*. In particular, the dendrogram using just the CO1 gene is a phenetic result, used for illustrative purposes, and is merely suggestive but is not a reliable phylogenetic estimate; a rigorous phylogeny using more genes and sophisticated phylogenetic analyses is recommended (Ramírez et al. 2010; Trunz et al. 2016; Packer and Ruz 2017).

The remarkable feature about this new species is its highly distinct clypeus, featuring the medial ridge and protuberance, which is unusual for *Leioproctus* (Maynard, 2014). Only the monotypic subgenus *Colletopsis* Michener 1965, and the two species in *L.* (*Ceratocolletes*) feature a median ridge on the clypeus, which is especially pronounced in *L. zephyr.* This feature invites speculation about its evolution and function. Present in both sexes, it is unlikely to be due to sexual selection (although there is the possibility of mutual sexual selection acting on this feature). The male is relatively robust and broad metasoma compared with some *Leioproctus* males, but still relatively slimmer than that of the female. Patterns of sexual dimorphism vary across bees, and the relative size of the sexes can be considered to be informative about the relative sexual and natural selective forces acting up on the species. The relatively larger size of the female suggests that *L. zephyr* is non-territorial (Alcock and Houston 1996; Paxton 2005). The protuberance, although present in both species, is slightly larger relative to the bee's head in the male (length of protuberance extending from clypeus in profile relative to head length 0.22 for the female compared with 0.29 for the male; see Supporting Information2), which may suggest a role for this protuberance in sexual selection. No instances of mating or nesting behaviour were observed but would be insightful for future studies.

The raised ridge and protuberance may be a point for muscle attachment of the mandibles (Grimaldi et al. 2005). X-ray micro-computed tomography (micro-CT) scans would shed light on whether this hypothesis has support. Another intriguing possibility is that this feature serves as a wedge to open up the keel of *Jacksonia* flowers. As a papilionaceous flower, the flowers of *J. sericea* have their fertile organs, and thus pollen and nectar "hidden" by a keel comprised of two ventral petals (Córdoba and Cocucci 2011). In order to access the floral rewards, pollinators must push down on the keel and the lateral petals of papillionate flowers (Córdoba and Cocucci 2011). This requires some force (Córdoba and Cocucci 2011), and it may be that the clypeus with its prominent protuberance of this specialised *Leioproctus* is used to wedge open the keel of its host flower. Although involving glossa or leg modifications rather than clypeus structure, other cases of unusual bee morphological structures have been linked to adaptations for accessing floral rewards in flowers that have limited access to flower visitors (e.g. Houston 1983; Pauw et al. 2017). Observations of other bee species have revealed behaviours that involve using the head and mouthparts to push or force themselves into flowers that have petal morphologies limiting access (Packer, 2004), including those with keeled flower parts (e.g. Westerkamp 1993; Raju and Rao 2006; Amaral-Neto et al. 2015). Although foraging observations were made in the field, the speed at which the bees foraged on flowers precluded being able to discern whether they performed this behaviour; specialised video-cameras recording this specie's foraging behaviour and analysed in slow-motion play-back would be able to evaluate support for this hypothesised function.

Leioproctus zephyr has an extremely limited range of flowers it will forage on, namely a subset of species within the genus *Jacksonia* (Suppl. material 1). This contrasts with most *Leioproctus* species, which are often highly polylectic (Maynard, 2014). A notable exception in this region of SWWA are three species that are specialised on

Conospermum (Proteaceae) (Houston, 1989). In this region where collections were made, most *Leioproctus* I collected or have observed have been recorded foraging on a range of Myrtaceae (*Corymbia*, *Callistemon*, *Eucalyptus*). The only other occurrence of a *Leioproctus* on a plant in the family Fabaceae was on *Acacia* (previously classified as a distinct family, Mimosaceae) (Maynard, 2014). Despite other *Jacksonia* (*J. sternbergiana* Bentham and *J. furcellata* Bonplande & de Candolle co-flowering, often in abundance, at sites where *L. zephyr* was collected, no specimens were ever observed foraging on these other related species.

The reason for this specialisation can only be speculated. It is unlikely to be due to avoiding competition, as *J. sericea* is frequently visited by *Megachile* Latreille 1802, a genus which is more typically associated with Fabaceae (Houston 2000; Prendergast and Ollerton 2021).

Leioproctus zephyr also appears to have a limited season of activity covering only two months in summer (December to January). The species was not observed after early January in the more recent collections by the author. Although the latest date the species has been collected was the end of January (January 19th), this was a single collection forty years ago. As temperatures have risen by almost 1 °C over the last century, and rainfall has declines of 15% since the mid-70s, and it may be that climate change (Climate Council 2014) means that temperatures are now too hot for this species to remain active at this later collection date (Prendergast, 2022). Climate change may post a threat to *L. zephyr* by causing mismatches between the phenology of the emergence of the bee and its host plant (Hughes 2003; Pyke et al. 2016; Schleuning et al. 2016; Settele et al. 2016; Prendergast 2022).

This new species appears to be restricted to native vegetation reserves in the southwest Western Australian biodiversity hotspot (refer to Fig. 3). The only other population the species has been collected from is Pinjarrega Nature Reserve, almost 200 km^2 away from the other sites and thus well outside the flight range of the species (Zurbuchen et al. 2010). Whether other populations exist in the intervening region is unknown, however as *J. sericea* occurs in the intervening area, targeted surveys are recommended. It is also unknown whether the species still persists at this location, as it has been over two decades since the three specimens have been collected from this location. If it were to become extirpated, re-colonisation is therefore unlikely.

Comprehensive surveys that I conducted over 10 months failed to record this species in any residential gardens, which can be attributed to the lack of suitable foraging resources. Even at bushland remnants were *Jacksonia sericea* was flowering, this did not guarantee the presence of this species: for example, Piney Lakes Reserve has *J. sericea* patches, and is approximately only 4 km away from Wireless Hill where this species was recorded, yet no records were made at Piney Lakes. *L. zephyrus* was also not recorded on *J. sericea* at other bushland remnants surveyed in the City of Bayswater in 2020–22 (Prendergast 2021, 2022b). This region has become highly fragmented due to urbanisation and the associated loss of natural habitat for road and urban development. Other studies outside of Australia have also found that specialist

species are underrepresented in small, isolated fragments in urbanised areas (Cane et al. 2006; Pauw 2007). Given the dependence of this new species on native vegetation remnants with *J. sericea*, efforts much be made to protect any native bushland that remains with these plants, and encourage bushland restoration initiative to plants patches of *J. sericea* to promote connectivity and increase the overall habitat area for this remarkable species.

There has been no formal conservation status of *Leioproctus zephyr*, but some recommendations can be made based on information regarding its distribution, phenology, habitat, and resource associations. 18 specimens have been collected by T. Houston along with 96 by the author (Suppl. material 1). The majority however (two thirds of all specimens) have been collected from a single site, Kings Park (Suppl. material 1). Moreover, it is unknown whether the species still exists at two of the sites surveyed by T. Houston, especially the site where the species was first collected (Neerabup National Park) in 1979, which is a great distance from where the other populations occur. *L. zephyr* is locally abundant at Kings Park, which is a large, intact area of remnant bushland that is under strong conservation legislation as an A-class Reserve, and is well-managed by the Government of Western Australia's Kings Park and Botanic Gardens Authority, with two-thirds of this 400.6ha park being protected as managed bushland (Botanic Gardens and Parks Authority 2017). One of the sites where *L. zephyr* was recently collected is marked to be undergoing partial destruction to make way for urban development (Young, 2018); ongoing urbanisation of the matrix surrounding sites may also affect populations through edge effects, by increasing isolation, and preventing metapopulation dynamics.

Further surveys during December and January in areas where *Jacksonia sericea* is flowering are required to establish this species extent of occurrence. Ongoing monitoring is also required to detect any population trends. Preservation of *J. sericea* is of utmost importance for this species.

Conclusion

Native bees are suffering from a major taxonomic crisis, and without a scientific name, understanding their distribution, abundance, and conservation status is a challenge, which is contributing to the poor state of conservation of invertebrates, including in a megadiverse country like Australia (Braby, 2018). Describing and naming this *Leioproctus* will enable it to receive conservation attention, as well as serve as a springboard for further taxonomic work on the diverse *Leioproctus* in Australia. This species is moreover morphologically distinct, featuring a modified clypeus, is oligolectic, and appears restricted to a few locations in the southwest Western Australian biodiversity hotspot. DNA barcoding has reinforced its distinct position and offers inspiration for further research into the taxonomy and systematics of Australian native bees and Hymenoptera at large.

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Supplementary material 1

Details of specimens of *Leioproctus zephyrus*

Authors: Kit S. Prendergast

Data type: COL

Explanation note: Collection details of specimens of *Leioproctus zephyr* sp. nov.

Link: https://doi.org/10.3897/jhr.93.85685.suppl1

Supplementary material 2

Morphological measurements

Authors: Kit S. Prendergast

Data type: excel file

Explanation note: Morphological measurements of specimens

Link: https://doi.org/10.3897/jhr.93.85685.suppl2

Supplementary material 3

Taxon ID tree

Authors: Kit S. Prendergast

Data type: png file

Explanation note: Taxon ID tree showing the relationship between *Leioproctus zephyr* sp. nov. in relation to other barcoded specimens generated in BOLD using the CO1 gene. Tree created in FigTree (http://tree.bio.ed.ac.uk/software/figtree/)

Link: https://doi.org/10.3897/jhr.93.85685.suppl3